The Dynamic Properties of Mammalian Skeletal Muscle

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ABSTRACT The dynamic characteristics of the rat gracilis anticus muscle at 17.5°C have been determined by isotonic and isometric loading. For a fixed initial length these characteristics were represented either as a family of length-velocity phase trajectories at various isotonic afterloads or as a series of force-velocity curves at different lengths. An alternate method of viewing these data, the length-external load-velocity phase space, was also generated. When the muscle was allowed to shorten from different initial lengths, the velocity of shortening achieved at a given length was lower for longer initial lengths. The amount of departure was also dependent upon the isotonic load, the greater the load the greater the departure. The departures were not caused by changes in the elastic elements of the muscle or fatigue in the ordinary sense. When the behavior of the muscle was investigated at different frequencies of stimulation, the shortening velocity was a function of the number of stimulating pulses received by the muscle at a given frequency. The shortening velocity of the rat gracilis anticus muscle is, therefore, not only a function of load and length, but also of an additional variable related to the time elapsed from onset of stimulation.

INTRODUCTION

The function of skeletal muscle is to contract, and in so doing to exert a force against its environment. The relation between the force the muscle can exert and the length of the muscle when it is stimulated tetanically under isometric conditions has been expressed by the length-tension diagram. When a muscle is permitted to shorten during stimulation, the velocity with which it begins to shorten is a function of the load imposed on the muscle. The familiar force-velocity curve, first described by Fenn and Marsh (1) and Hill (2), describes this relation. However, there is a family of force-velocity curves, depending on the length from which shortening begins. The relation between velocity and length throughout the complete excursion from initial to final length has been displayed by Carlson (3) for frog sartorius muscle and by

Sonnenblick (4) for cat myocardial papillary muscle as phase plane trajectories. A family of these phase plane trajectories is generated by allowing the muscle to shorten against different isotonic loads. Thus there is a complicated interrelationship among velocity of shortening, muscle length, and force.

Most of the data on the performance of skeletal muscle have been obtained from amphibian muscle, particularly the frog sartorius. However, to a lesser extent, studies of mechanics of isolated mammalian muscle have also been made, e.g. Ritchie (5), Close (6), and Wells (7). Because quantitative data on the mechanics of muscle form the basis for critical examination of hypotheses concerning muscle contraction, a series of experiments was undertaken to determine the dynamic characteristics of an isolated mammalian skeletal muscle.

Our present aim is to define the length, velocity, and force relationship of the contractile component of a tetanically stimulated in vitro mammalian skeletal muscle, the rat gracilis anticus. Since observations were made on whole muscle, noncontractile elastic elements were included in the analysis. Operationally, the noncontractile series elastic component was considered that element of the muscle which responds to an instantaneous decrement of load and the contractile component that element of the muscle responsible for the length, velocity, and force relationship after the effect of the series elastic component is removed computationally. Over the range of length in these experiments, the parallel elastic component was demonstrated to be negligible and was therefore ignored.

Experiments were performed to obtain the length-tension curve under isometric conditions, the extension-load relationship of the noncontractile series elastic component, and the isotonic length-velocity phase characteristics of the muscle at different initial lengths and loads. The results were fitted together to yield a three-dimensional representation of the interdependence among length, velocity, and force for mammalian skeletal muscle. Since the rat gracilis anticus is a thin, parallel fibered muscle with myofibers extending the entire length of the muscle and varying by less than 6 % in over-all length, it is particularly suited for such studies.

METHODS

Preparation

The experiments were performed on the right gracilis anticus muscle from white male Wistar rats (Carworth Farms Type CFN), approximately 50 days old, 140–165 g body weight, fed a normal balanced rat diet. The muscle has a mean wet weight of 60 mg (range, 45 to 90 mg) and a mean rest length of 2.7 cm (range, 2.4 to 3.0 cm).

The gracilis anticus is a long, thin (approximately $\frac{3}{4}$ mm), parallel fibered muscle which takes its origin from the posterior half of the pubic symphysis and is inserted

into the upper part of the crest and medial border of the tibia. It was removed as follows: the rat was anesthetized by an intraperitoneal injection of sodium pentobarbital, 45 mg/kg. An incision was made in the skin from the midpoint of the tibia to the thigh and the skin displaced from the superficial fascia. The superficial fascia was removed and the muscle freed from neighboring muscles. The gracilis anticus, with a portion of the tibia and pubis, was placed immediately in a 1500 ml bath (16.5° to 17.8°C) containing oxygenated (95% O_2, 5% CO_2) bicarbonate-buffered Krebs-Ringer's solution pH 7.3 (NaCl, 116.8 mM/liter; $NaHCO_3$, 28 mM/liter; $CaCl_2$, 2.5 mM/liter; $MgSO_4$, 3.1 mM/liter; KCl, 3.5 mM/liter; KH_2PO_4, 1.2 mM/liter; and glucose, 11.1 mM/liter). The muscle was trimmed and small stainless steel yokes were attached to the pubis and tibia bones by means of "00" noncapillary braided black silk suture. These yokes were then placed between the lever member and the force transducer. Since the rat gracilis anticus muscle has relatively short tendons (normally less than 4% of rest length at the tibial end and less than 3% of rest length at the pubic end) and the remaining parts of the pubis and tibia are moderately stiff, the interconnection between muscle and lever system adds little series compliance to the total system.

Histological experiments upon randomly selected muscles incubated at rest length for 3 hr in a 30% weight/volume nitric acid solution to break down connective tissue indicated that most myofibrils were of a length consistent with myofibers that run from tendon to tendon. Other gracilis anticus muscles, quick frozen at rest length, were incubated in a medium that detected the presence of the enzyme succinic dehydrogenase. This study showed that although both fast and slow twitch myofibers are present in the gracilis anticus, most of the effective cross-sectional area is occupied by fast twitch myofibers. The method of classification was that proposed by Henneman and Olson (8).

Lever System

The muscle lever used in this study (equivalent mass 350 mg, compliance 3.5 10^{-7} cm/dyne) consisted of an electromechanical torque source and lightweight (12.5 cm) magnesium lever. The force transducer was constructed of a low mass, aluminum alloy cantilever beam that was deformed by the muscle. The deflection of the cantilever was measured by a linear motion transducer. The loaded resonant frequency of the force transducer was 350 cps. The velocity transducer was constructed of a small galvanometer coil mounted on the shaft of the torque source. Since muscle velocity is proportional to angular velocity, this device produced a voltage proportional to muscle velocity with no inherent phase lag. Changes in length of the muscle were obtained by integrating the output of the velocity transducer with a low noise, low drift operational amplifier integrator. A detailed description of this lever system has been published elsewhere (9).

The muscle was stimulated supramaximally by two platinum multielement electrode assemblies which set up an electric field normal to the long axis of the muscle (current density $\simeq$ 0.08 amp/cm^2).

Experiments were performed using trains of from 14 to 40 pulses of 2 msec duration with separations of from 10.0 to 16.5 msec. All records were displayed on a

Tektronix RM561A oscilloscope and recorded on Polaroid type 107 film. The recording oscilloscope was intensity modulated in all experiments by the stimulating pulses.

The lever system has the advantage that it permitted the following experiments to be performed without removing the muscle from its original attachments.

Isometric

Experiments under isometric conditions were repeated at ¾ hour intervals on all muscles at lengths selected randomly from a range of about 0.7 to 1.2 times rest length, L_o. L_o is defined as the length at which maximum force, P_o, is developed.

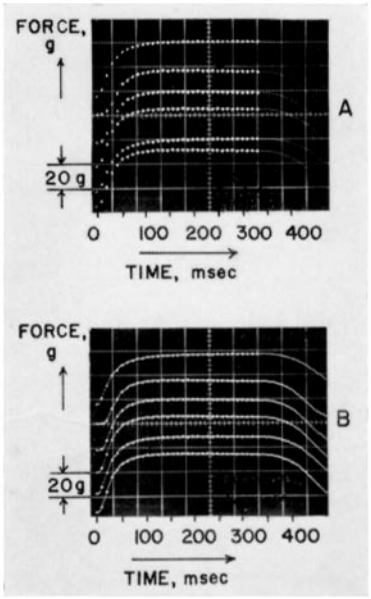

FIGURE 1. Isometric force-time curves. Base line has been displaced for each record. Cathode ray tube intensity modulated by stimulating pulses. Experiments in upper frame (A) performed 3 hr before experiments in lower frame (B). Curves in upper frame (A): muscle lengths in centimeters as performed, from bottom to top, 2.6, 3.2, 2.8, 2.4, 2.2, and 3.0. Curves in lower frame (B): muscle lengths in centimeters as performed, from bottom to top, 2.8, 3.0, 2.6, 2.4, 2.2, and 3.2. 1 min recovery was allowed between each isometric experiment. Muscle weight = 80 mg; L_o = 2.8 cm; P_o = 47.5 g; stimulating frequency = 98 pulses per sec; bath temperature = 17.5°C.

A typical example of such an experiment is displayed in Fig. 1. At a given length, the tension developed during the plateau of the tetanus (approximately 180 msec after the onset of stimulation) was the value used in the length-tension plot. Reproducibility of this isometric length-tension curve, recorded as the difference between the over-all response of contracting muscle and the passive response of muscle stretched while unstimulated, served as a measure of the viability of the preparation. Experiments under isotonic conditions were always bracketed by these isometric experiments; if there was a change of more than 15% from the initial length-tension curve, the experiment was terminated. The preparation could fulfill this requirement of reproducibility for 3 hr or more.

Isotonic (Length-Velocity Trajectories)

Experiments under isotonic afterloaded conditions were performed with a preload not exceeding 3 g. In some experiments, the initial length was kept constant and the muscle was required to shorten against six or seven isotonic afterloads, varied at

random. In other experiments, the isotonic afterload was kept constant and initial length was varied at random. Isotonic experiments were also performed at fixed initial length and load, varying frequency of stimulation. All records obtained from these experiments were recorded in the form of length-velocity phase trajectories.

Quick Release

Experiments to determine the series elastic component were performed by releasing a supramaximally stimulated muscle from isometric tetanic conditions to some fixed

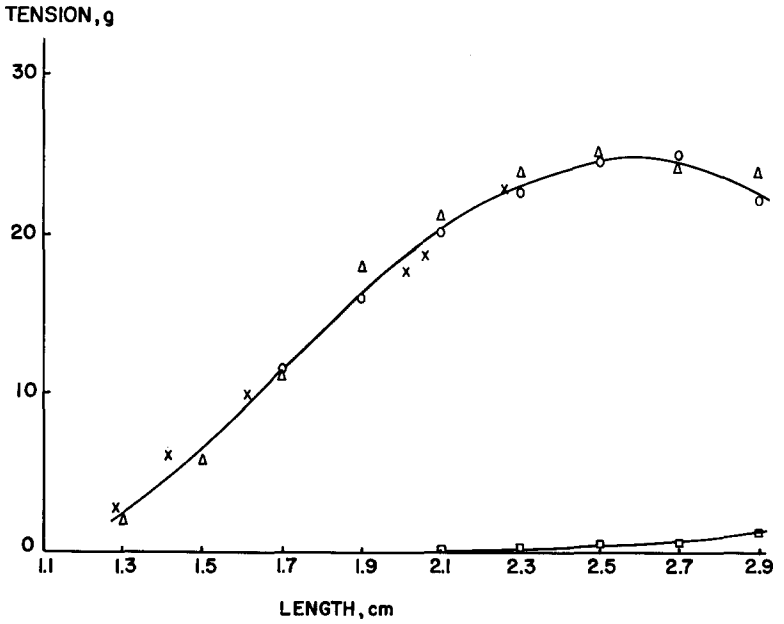

FIGURE 2. Isometric length-tension curve, indicating the character of the relationship at lengths much shorter than L_o. Circles are experimental points from initial isometric experiments. Triangles are the results of isometric experiments performed 1½ hr later. X's indicate the end points of isotonic shortening from an initial starting length of 2.4 cm. Squares indicate points from resting length-tension experiments. Sequence of experiments was selected randomly. Muscle weight = 50 mg; L_o = 2.6 cm; P_o = 25 g; stimulating frequency = 95 pulses per sec; bath temperature = 17.6°C.

isotonic load. These releases took place in less than 4 msec. The amount of instantaneous shortening for the decrement in load (amount of the quick release) is taken as the change in length of the series elastic component corrupted by the compliance and mass of the lever system (10).

RESULTS

Isometric

The isometric tetanic length-tension curve for a typical rat gracilis anticus muscle is shown in Fig. 2. This curve was similar from preparation to prepara-

tion when the muscle was not stretched past 130 % of rest length. In 28 rats, the mean maximum isometric tetanic tension expressed in force per gram of muscle was 480 g/g (SD ± 28). This mean tension expressed in force per unit of area was 1.34 kg/cm^2 (SD ± 0.1). In computing the force per unit of area, the muscle is assumed to be a regular parallelepiped and thus the cross-sectional area of the muscle was given by the relationship m/L_o, where m is the mass of the muscle. Histological experiments showed that for quick frozen muscles this method overestimated the cross-sectional area by about 10 %.

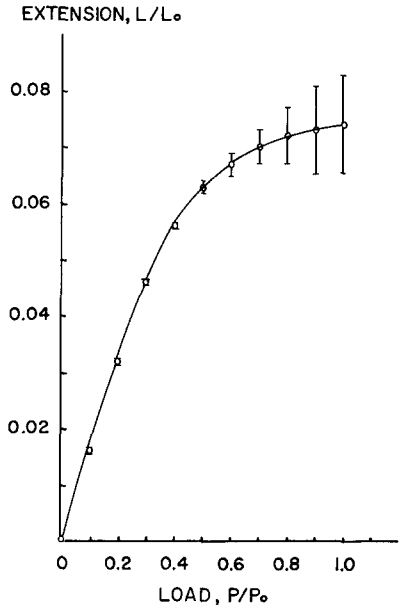

FIGURE 3. Stress-strain curve of the series elastic component. Means of five muscles ± 1 SD.

Series Elastic Properties (Quick Release)

The stress-strain properties of the series elastic component were determined on five muscles by a method similar to that developed by Wilkie (10). A muscle, stimulated tetanically and supramaximally under isometric conditions, was released suddenly and permitted to shorten against a fixed but lesser load. At lengths less than 1.1 L_o the parallel elastic component made no appreciable contribution to the response. If the release were instantaneous, the series elastic component, since it is only lightly damped, would shorten to its full capacity before the contractile component began to shorten. In practice, however, release cannot be instantaneous because the lever system has finite mass. This delay permits the contractile component to contribute to the initial shortening. Corrections for this departure from the ideal are described elsewhere (11). These corrections increase the magnitude of the series elastic component by 13 %.

The amount of instantaneous shortening, corrected for the lever system, plotted against the decrement in load from isometric to isotonic conditions, describes the stress-strain curve (Δ length–Δ tension) of the series elastic component. This stress-strain curve appears in Fig. 3. From this figure, the series elastic component is seen to have a maximum extension of about 0.07 L_o when P_o is impressed across it. Thus the series elastic component of the rat gracilis anticus muscle is more compliant than that typically found in the frog sartorius muscle (10). This increased compliance could reflect a distortion of both the tibia and pubis bones which are attached to the yokes of the lever system or the effect of the tendons which comprise about 6 % of the muscle preparation. The contribution of the series elastic component to muscle

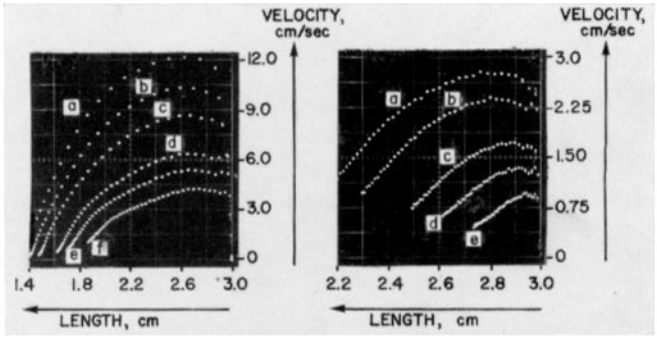

FIGURE 4. Family of afterloaded isotonic length-velocity phase trajectories. Constant initial length (3.0 cm), varying P. Initial length 2 mm longer than rest length. Shortening to the left. Cathode ray tube intensity modulated by stimulating pulses. Curves to the left: isotonic loads in grams, *a*, 2.8; *b*, 3.8; *c*, 6.0; *d*, 8.9; *e*, 10.7; *f*, 13.4. Curves to the right: isotonic loads in grams, *a*, 17.5; *b*, 19.6; *c*, 21.3; *d*, 22.8; *e*, 24.5. Muscle weight = 76 mg; L_o = 2.8 cm; P_o = 34.8 g; stimulating frequency = 95 pulses per sec; bath temperature = 17.5°C.

length at a given external load was subtracted from the over-all muscle length in order to determine the relation between the velocity of shortening and the length of the contractile component, L', in the series of experiments shown in the next section of the results.

Isotonic (Length-Velocity Trajectories)

Fig. 4 displays a family of length-velocity phase trajectories, obtained from a single muscle stimulated to shorten from the same initial length with varying afterloads. Similar experiments were performed on 10 muscles. The experiments shown in Fig. 4 were terminated after 420 msec of stimulation, which was too brief to permit complete shortening with the muscle under heavier loads. If the muscle had been stimulated for a longer period of time, it would have eventually shortened to the isometric length-tension curve, despite the

appearance of the length-velocity phase trajectories curtailed before shortening was complete. In reaching this final length, the velocity of the muscle would have shown decreasing deceleration; that is, there would be a terminal upward concavity of the velocity function. That the muscle does shorten to the length predicted by the isometric length-tension curve was verified by permitting muscles to shorten to completion. The final length reached by the muscle shortening against a given load coincided with the isometric length-tension curve obtained for that muscle before and after the series of isotonic experiments (Fig. 2), so long as the initial length of the muscle was less than 1.2 L_o. There are thus three phases exhibited by the length-velocity phase trajectory: a rapid initial rise in velocity associated with nearly iso-

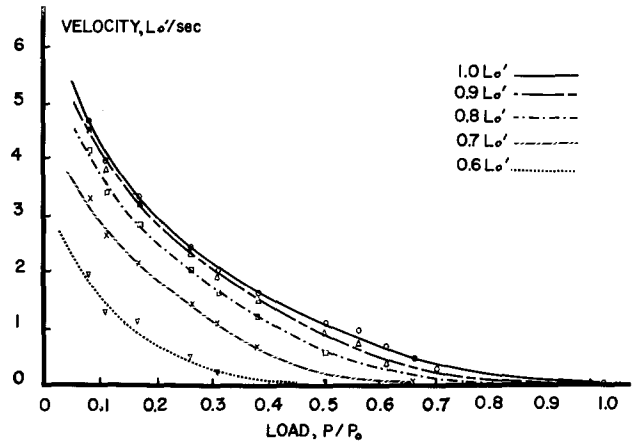

FIGURE 5. Normalized isotonic force-velocity curves of the contractile component at various lengths of the contractile component. Fixed initial muscle length of 3.0 cm. Load normalized by division by P_o. Same muscle as in Fig. 4.

metric contraction, a phase of relatively rapid deceleration, and a terminal phase of small, decreasing deceleration.

The length-velocity phase trajectory of the contractile component can be obtained by correcting curves such as those shown in Fig. 4 on the basis of the stress-strain curve of the series elastic component. At light loads, there is almost no correction. At heavier loads, the observed length is decreased by about 5 %. For example, if the length at which a muscle develops its maximum tension, P_o, is L_o = 2.8 cm, and if at this tension the extension of the series elastic component is 2 mm, then the length of the contractile component, L_o', is 2.6 cm. The effect of such correction of the curves of Fig. 4 is to shift the length at which maximum velocity occurs toward L_o'. For loads less than about 0.6 P_o, maximum velocity of shortening of the contractile component occurs at L_o'. For greater loads, maximum velocity appears to

occur at lengths greater than L_o', but this deviation will be shown to be related to the dependency of velocity on the number of stimuli.

The force-velocity curve of the contractile component may be obtained from Fig. 4, by plotting, at a fixed contractile component length, velocity as a function of load. It is therefore possible to construct the family of force-instantaneous velocity curves at constant contractile component length, as shown in Fig. 5. Because maximum velocity occurs at L_o' for loads less than 0.6 P_o, and at lengths greater than L_o' for heavier loads, the force-velocity

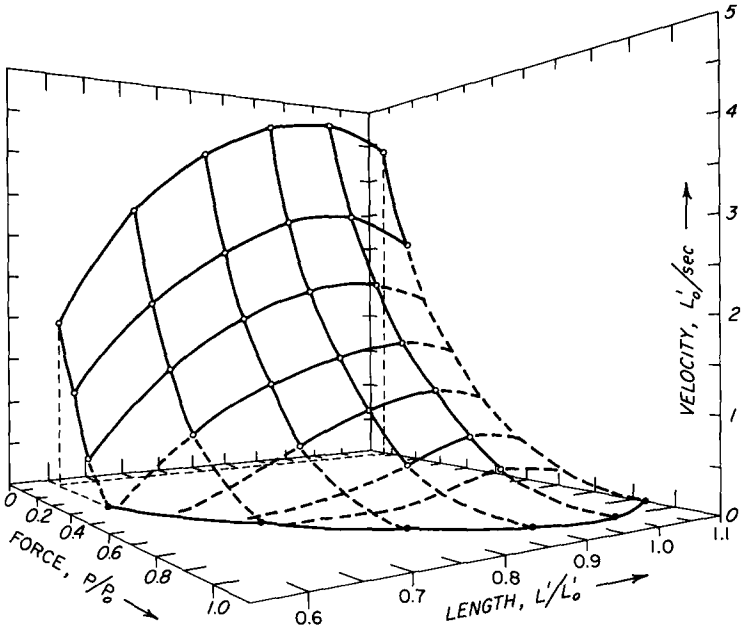

FIGURE 6. Three-dimensional representation of the dynamic length–force–velocity phase space of the contractile component.

functions for lengths less than L_o' all occur below the one obtained at L_o'. At lengths greater than L_o', the velocities are less than those at L_o' for loads smaller than 0.6 P_o, but the relationship is obscured at higher loads for reasons to be discussed later.

Fig. 6 is a three-dimensional representation of the dynamic length–force–velocity phase space of the contractile component, constructed from isometric length-tension curves and from length-velocity phase trajectories. The base of the volume is the isometric length-tension curve; that is, the relation at zero velocity. The force-velocity curves are shown at several contractile component lengths and the length-velocity phase trajectories are shown for several isotonic loads. A family of length-force curves (not given except for zero velocity) can be imagined at values of constant velocity.

Effect of Initial Length on Length-Velocity Phase Trajectories

Because maximum velocity did not occur at L_o' for loads greater than about 0.6 P_o with initial muscle lengths slightly longer than L_o, the relation between velocity, length, and tension was examined further in 17 muscles in which shortening occurred under constant load from different initial lengths. Results of such an experiment are illustrated in Fig. 7. At light loads the curves

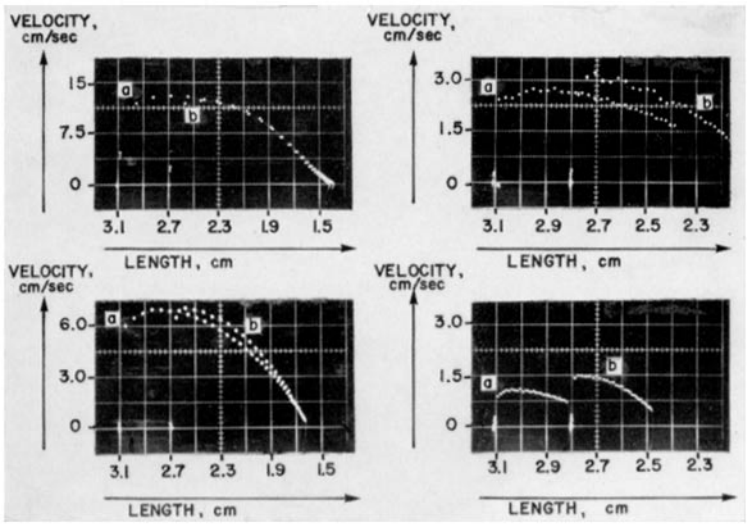

FIGURE 7. The effect of changes in initial length on the length-velocity phase trajectories. Direction of shortening is to the right. Cathode ray tube intensity modulated by stimulating pulses. Curves in the upper left: isotonic load, 3.2 g; initial lengths: *a*, 3.1 cm and *b*, 2.7 cm. Curves in the upper right: isotonic load, 19 g; initial lengths: *a*, 3.1 cm and *b*, 2.8 cm. Curves in the lower left: isotonic load, 10 g; initial lengths: *a*, 3.1 cm and *b*, 2.7 cm. Curves in the lower right: isotonic load, 33 g; initial lengths: *a*, 3.1 cm and *b*, 2.8 cm. Muscle weight = 79.5 mg; L_o = 2.8 cm; P_o = 47.5 g; stimulating frequency = 95 pulses per sec; bath temperature = 17.6°C.

coincided so that velocity became a function only of muscle length, independent of the initial length. As the load increased, the velocity of the muscle shortening from the shorter length became greater at any given length than the velocity of the muscle under the same load but with a longer initial length. The difference in velocities was small at moderate loads and increased as load increased.

When the muscle begins shortening from a longer initial length it obviously takes more time to reach any given length than when it begins shortening from some intermediate length at the same load. It is also true that for a constant frequency of stimulation, the muscle shortening from the longer initial length has received more stimuli. The question of whether the decrease in velocity such as appears in Fig. 7 is due to the passage of time or to the num-

ber of stimuli was examined by stimulating each of five muscles at two different tetanizing frequencies, 65 and 95 pulses per sec. Velocity of shortening was less at the higher frequency for any given load and initial length, and separation of the phase trajectories for a muscle stimulated at the same load but from two different initial lengths was greater at the higher frequency of stimulation (Fig. 8), provided that the muscle stimulated at 95 pulses per sec received at least four more stimuli to reach a given length than it received at 65 pulses per sec.

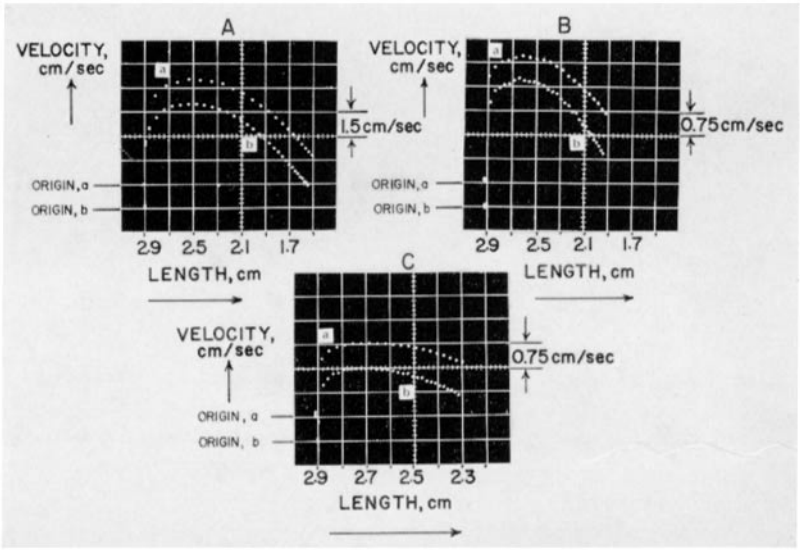

FIGURE 8. The effect of stimulating frequency on the shape of the length-velocity phase trajectories. Shortening to the right. Stimulating frequency of curve *a* in each frame is 65 pulses per sec. Stimulating frequency of curve *b* in each frame is 95 pulses per sec. Cathode ray tube intensity modulated by stimulating pulses. Initial length 2.9 cm. Isotonic load, upper left frame (A), 3 g; upper right frame (B), 5.8 g; lower frame (C), 9 g. Muscle weight = 44 mg; L_o = 2.5 cm; P_o = 25 g; bath temperature = 17.6°C

The relation between decrement in velocity and number of pulses was quantitated as follows. Each phase trajectory was divided into a series of equal length divisions. At each of these divisions the difference in number of stimulating pulses, ΔN, received by the muscle up to that length (95 pulses per sec minus 65 pulses per sec) and the difference in velocity, Δv, between each of the sets of phase trajectories, were calculated. The difference in velocity obtained at each of these length increments was then normalized by dividing this difference by the maximum velocity attained in the phase trajectory. Data obtained from one experiment are displayed in Fig. 9. If the phase plane trajectories were superimposable, the curve would always be zero-valued. A negative value of $\Delta v/v_{max}$ for any given ΔN indicates that

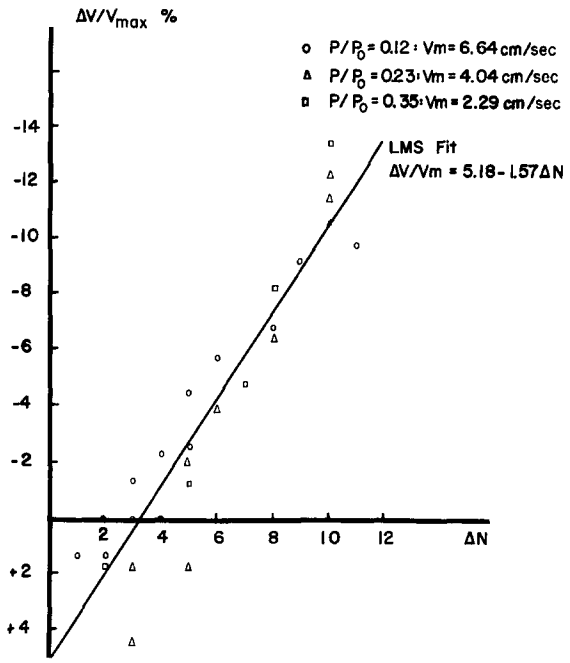

FIGURE 9. The relationship between the difference in the number of accumulated stimulating pulses, ΔN, received by the muscle (95 pulses per sec–65 pulses per sec), and the difference in velocity, Δv, between the phase trajectories divided by the maximum velocity, v_{max}, achieved in the phase trajectory. ΔN increases at a rate of 30 pulses per sec; therefore, the abscissa is 30 times time in sec. Muscle weight = 44.5 mg; L_o = 2.6 cm; P_o = 25 g; bath temperature = 17.6°C.

TABLE I

EFFECT OF NUMBER OF STIMULATING PULSES ON VELOCITY OF SHORTENING

Muscle	1	2	3	4	5	Mean	SD
Slope $\%\, v_{max}$/pulse	−1.25	−1.25	−1.36	−1.58	−1.59	−1.41	0.141
Intercept $\Delta v/v_{max}$	0.0574	0.0337	0.0545	0.0518	0.0635	0.0522	0.0105
Correlation coefficient	0.866	0.932	0.699	0.866	0.629	0.798	0.118

See text for description of analysis. ΔN is the difference between the number of pulses delivered at 95 and at 65 pulses per sec at the instant the muscle reached any given length. Δv is the difference between the velocity of muscle at that length in response to 95 pulses per sec and its velocity in response to 65 pulses per sec. v_{max} is the maximum velocity during shortening. Data obtained on each of five muscles were treated by conventional least mean square analysis to obtain the best linear form. The equation for the average response of the five muscles is $\Delta v/v_{max} = 0.052 - 0.014 \cdot \Delta N$.

the velocity at a stimulating frequency of 65 pulses per sec was higher than the velocity at a stimulating frequency of 95 pulses per sec and that the magnitude of $\Delta v/v_{max}$ was an indication of the degree of separation.

A linear relationship exists between ΔN and $\Delta v/v_{max}$ (significant to $P \leq$

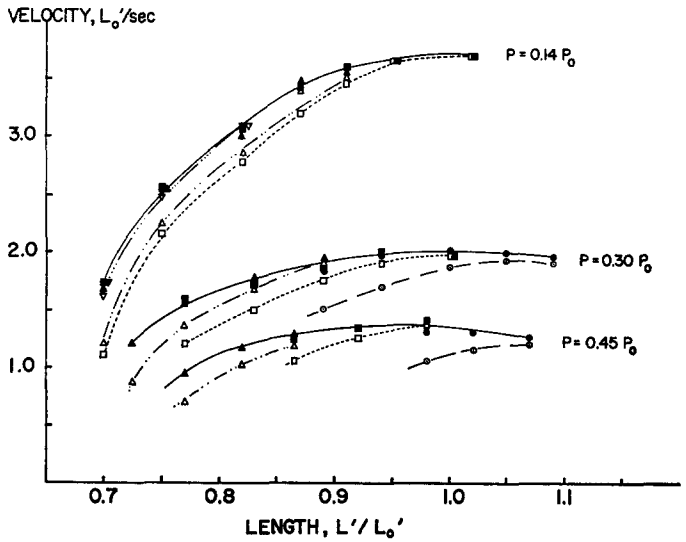

FIGURE 10. The effect of applying the relationship between ΔN and $\Delta v/v_{max}$, shown in Fig. 9, on a series of length-velocity phase trajectories at three isotonic loads. Open symbols and dashed lines are experimentally observed length-velocity phase trajectories, with velocity normalized in units of L_o'/sec and length normalized in units of L'/L_o'. The three isotonic loads are indicated by P, given as a fraction of P_o. There were three initial lengths at each load. At a given isotonic load, each of the three length-velocity phase trajectories beginning at different lengths is indicated by a different open symbol. When the value for each experimental point is corrected by the relationship between ΔN and $\Delta v/v_{max}$, the calculated value is indicated by a filled symbol corresponding to the open symbol. All filled symbols at each isotonic load fall on a single line, shown by the solid curves. For the calculation the line in Fig. 9 was extended to $\Delta N = 16$. Muscle weight = 54 mg; L_o = 2.55 cm; P_o = 28.7 g; stimulating frequency = 80 pulses per sec; bath temperature = 16.8°C.

0.001). Results of this analysis are shown in Table I. In general, velocity decreased by 1.4 ± 0.14 % of v_{max} per pulse. This linear relationship indicates that the shortening velocity of the contractile component is a function of the number of stimulating pulses received by the muscle at a given frequency, over the range of pulses actually administered. At moderate loads to accumulate a ΔN of 12 (the limit of Fig. 9), the muscle shortens over most of its physiological range. ΔN of greater than 12 requires excessive stimuli for heavily loaded muscles or severe shortening for moderately and lightly loaded muscles. For this reason, it was difficult to obtain ΔN greater than 12. Ob-

viously, because velocity goes to zero when shortening stops, Δv must also go to zero. Therefore, the linear relation shown in Fig. 9 cannot in fact hold for all values of ΔN. It is also unwarranted, and indeed unlikely, that the same linear relation holds for all ranges of frequency of stimulation from fusion frequency (55 pulses per sec at 17.5°C) to those frequencies that fatigue the isometric force-time curves (greater than 110 pulses per sec at 17.5°C).

It is possible to exploit the effect of the number of pulses on the decrease in velocity of shortening to develop velocity as a function only of length and tension. Despite the fact that the relation between number of pulses and decrease in velocity shown in Table I was obtained at stimulation frequencies of 65 and 95 pulses per sec, the relation given in this table was applied to reconstruct the phase plane trajectories shown in Fig. 10 in response to stimuli at 80 pulses per sec. The velocity at every experimental point in Fig. 10 was increased by the value corresponding to the ΔN given in Table I. This reconstruction yielded identical values for the phase trajectories at a given load, independent of initial length.

DISCUSSION

The present experiments show that the mechanical response of mammalian skeletal muscle may be analyzed by the same methods used for frog muscle. One of the as yet not fully explained properties of frog muscle was found to exist in mammalian muscle; specifically, the velocity of shortening depended not only upon the length of the muscle and on force or external load but also on some variable related to the time elapsed from the onset of stimulation. In the rat gracilis anticus muscle, the velocity of shortening appears to be a function of the number of impulses delivered to the muscle. The departures of the phase trajectories do not appear to be related to changes in elastic elements since the peak velocities are different for different initial lengths; a change in the internal elastic elements would merely tend to shift the maximum velocity and not alter its magnitude. Nor do the departures appear to be due to fatigue in the ordinary sense since the isometric force-time curves do not deteriorate with time (Fig. 1). Thus, the velocity of shortening under a given load and frequency of stimulation is smaller at any given absolute length for a muscle shortening from a longer initial length than from a shorter initial length. The more stimuli required for a muscle to reach a length, the smaller its velocity of shortening will be at that length.

A method has been developed for mammalian muscle that allows the velocity of shortening to be corrected to eliminate the effect of stimulation. Symbolically we may say

$$\dot{L}' = f(L', P, S)$$

where S is the frequency of stimulation. Experimentally for the rat gracilis anticus at 17.5°C

$$\dot{L}' = f_1(L', P) f_2(S)$$

where $f_1(L', P)$ is some nonlinear function of length and load, independent of stimulation, and $f_2(S)$ is the stimulation correction factor. Furthermore,

$$f_2(S) = 1 \qquad 0 \leqq t < 4/S$$

and

$$f_2(S) = (1 - 0.014\ S\ t) \qquad 4/S \leqq t \leqq 12/S$$

where t is the duration of stimulation. A relation for the corrected instantaneous velocity emerges from these expressions since

$$\frac{\dot{L}'}{f_2(S)} = V = f_1(L', P)$$

where V is the initial length-independent velocity and $f_1(L', P)$ is a function similar to that investigated by Carlson (3) and Bahler et al. (12).

The time-independent phase trajectories generated by this technique (see Fig. 10) decay less rapidly than the experimental phase trajectories. These length-independent trajectories presumably indicate the velocity of which the muscle is capable at a given load and length if it is not modified by previous stimulation. The significant point in this procedure is that when activation is not a problem, velocity is independent of initial muscle length.

Experimentally, when the rat gracilis anticus muscle is stretched past 130 % of L_o, the shape of the isometric length-tension curve changes. This irreversible change takes place at a length at which the muscle still produces considerable force. Although this phenomenon has also been observed in whole frog sartorius muscle (3), it does not occur in the single frog muscle fiber preparation (13). This property of whole muscle preparations might be caused by a rupturing of the sarcolemma from changes in the inert parallel elastic components due to stretching or by the effects of a spectrum of different sarcomere lengths within the myofibers at these long muscle lengths damaging individual contractile units. Although the first of these two possibilities is the most plausible, the exact mechanism of this phenomenon cannot be identified within the context of the present experiments.

When the dynamic performance of tetanically stimulated rat fast muscle is compared with that of other striated muscles, several interesting points emerge. First, the shapes of the individual phase plane trajectories of mammalian skeletal muscle are qualitatively similar to those obtained from frog muscle (3) and mammalian papillary muscle (4). Second, if the initial length of a tetanically stimulated frog muscle (14) or mammalian muscle is varied, the instantaneous velocity of shortening at any given length, in addition to being a function of length and load, is also a function of a variable related to this initial length. Third, isotonically loaded frog (3) and mammalian skeletal muscle will shorten to the isometric length-tension curve so long as the muscle has not been stretched to more than 1.2 L_o. Finally, shortening skeletal muscle has three phases: an initial phase in which the muscle rapidly

accelerates, an intermediate phase in which the muscle gradually decelerates (for initial lengths about L_o), and a final stage in which the muscle virtually creeps to its final length (15).

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